EFFECT OF WATER CURRENTS UPON THE ATTACHMENT AND GROWTH OF BARNACLES [1]

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Introduction

There exists a considerable body of published work dealing with peculiarities in the distribution of sessile marine invertebrates in general, and, although experimental evidence is incomplete some speculation has been offered as to the manner in which their distribution is limited by various factors of the environment which influence their attachment and growth. The object of the present studies was to investigate the action of the water current factor by experimental methods, with particular reference to the species of barnacles which are most abundant in the Miami area.

Much of the earlier work on sessile marine animals has been reviewed by Mc Dougall (1943), and need not be considered here in detail. A bibliography of investigations dealing with sessile organisms from the point of view of ship fouling is given by Neu (1933), and an excellent general account of marine fouling by Visscher (1928) who does not, however, include more than a brief reference to the effect of water currents.

The effects of environmental factors have been deduced from the results of ecological surveys by a number of investigators. Stephenson and his co-workers, in a series of publications entitled *The South African Zone and Its Relation to Water Currents* (see bibliography), Fischer-Piette (1928, 1928a), Pierron and Huang (1926), and Prennant and Teissier (1924) have described the populations of rocky shores and the distribution of sessile organisms in general, but with scanty reference only to the relation between barnacle attachment and the velocity of water currents. Stephenson and Bright (1938) and Stephenson and du Toit (1937), however, note the absence of certain species of barnacles from surfaces exposed to heavy wave action.

The possibility of water movement influencing barnacle attachment is suggested by Fischer-Piette (1932) in his reports on surveys of the shores of the English Channel. Shelford and Towler (1925), Towler (1930), and Newcombe (1935) have paid particular attention to barnacles in associations of Balanus-Littorina and Balanus-Mytilus and draw attention to the more luxuriant growth of barnacles exposed to strong water currents, particularly in shallow water. The role of water currents is also mentioned briefly in accounts of ecological surveys by Rice (1930), Moore (1935a), and Moore and Kitching (1939), who stress the part played by

[1] These experiments were conducted while the author was engaged by the Woods Hole Oceanographic Institution in investigations under contract with the Bureau of Ships, Navy Department, which has given permission to publish the results. The opinions contained herein are those of the author and do not necessarily reflect the official opinion of the Navy Department or of the Naval service at large.

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them in the provision of an adequate food supply, as well as the adverse effects of wave action.

Experimental investigation has yielded more direct information. Moore (1933) studied the effect of currents upon the attachment of cyprid larvae with particular regard to orientation, but gives no estimate of current velocities which limit attachment. The related phenomena of wave action are considered by Moore in a separate paper (1939).

Evidence as to the effect of water currents is also afforded by the study of ships and other objects moving through the water. The economic importance of ship-bottom fouling has stimulated this kind of observation. Heutschel (1934) and Neu (1932) state that vessels collect barnacles most readily when in harbor and when subjected to relatively less water movement. Visscher (1930) further observes that barnacles are usually killed during ocean passages of about 500 miles. Hiraga (1934) showed experimentally that, in the laboratory, 10 to 17 day old barnacles were lost during a five day exposure of test planks to water currents, whereas twenty-four day old barnacles remained alive and intact. In a later paper of Visscher (1938) he concludes that barnacles are not distributed by ships. This is contrary to the views of Fischer-Piette (1929, 1935) who expresses the opinion that *Balanus amphitrite* found by him on the coast of France, was brought from the tropics on the hulls on ships. Later observations by Phelps (1942) on test panels support the conclusion that excessive water currents inhibit the attachment and growth of barnacles.

The extensive observations of McDougall on the pile fauna at Beaufort include the results of exposing various types of experimental collecting apparatus. His experiments on the effect of water currents indicate that fewer barnacles settle and that growth is slower in more rapid currents. His results did not, however, give an accurate indication of limiting or optimum velocities to which his collectors were exposed.

The experiments which form the subject of the present account are divided into a study of the effects of water currents upon the attachment of cyprid larvae, and into a consideration of the effects of water currents upon the organisms following attachment. Under natural conditions of fluctuating tidal currents and wind drifts it is conceivable that a cyprid might attach during a period of minimum water flow in a particular region and that, once attached, the maximum flow would be insufficient to detach it or to inhibit its growth. The aim of the investigation was to establish the limiting velocities of current for initial and continued attachment and growth.

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Methods

In order to study the effects of water currents two types of apparatus were designed which would permit the movement of sea-water relative to the experimental surface at predetermined and variable velocities. The first consisted of a rotating disc, immersed in the sea. The second type of apparatus consisted of a series of glass tubes of varying cross-sectional diameter. The rotating disc was employed both in the study of initial attachment of barnacles and in the study of growth subsequent to attachment. The glass tubes of graded diameter were employed in the observations on initial attachment only, as a check against results obtained with the rotating disc.

Water Currents and Attachment on the Rotating Disc

The rotating disc apparatus as used in the experiments here described is essentially similar to a machine described by LaQue (1943) for the purpose of studying the effect of sea-water currents upon corrosion of metal samples, with certain changes in design appropriate to the particular use to which it was put. The modified machine consists of a vertical shaft rotated by means of an electric motor and a system of belts and pulleys. The disc is attached to the shaft by means of a flange and small brass screws and is maintained in a position several inches below low water spring tide. At velocities of rotation used in the experiment no cavitation occurred at this depth.

By changing the arrangement of pulleys the speed of rotation may be varied up to approximately 1750 r.p.m. The rate of movement in knots of any portion of the disc relative to an imaginary stationary body of water is readily calculated as approximately $R \times D / 370$, where R is the number of revolutions per minute and D the diameter in inches. This velocity is nominal, however, and does not accurately represent the rate of relative movement between the disc and the water close to its surface. Frictional drag and centrifugal forces produce vortex movements which cause water to flow in a close spiral roughly parallel to the plane of the disc. As a result, the actual flow of water at any part of the disc's surface is less than the nominal rate calculated from the velocity of rotation. Size of the discs used varied up to 28 inches in diameter.

Experimental procedure consisted of bolting a new rotating disc on the shaft and setting the machinery in continuous operation. The disc was removed and examined at suitable intervals. At the same time a similar stationary disc was immersed at a point nearby the rotating disc, at the same depth and resting similarly in a horizontal plane. Observations on the second disc acted as a control for such factors as abundance of organisms, nature of the surface of the disc, etc. The apparatus was used at the edge of a covered slip at the Miami Beach Boat Corporation, where fouling is usually severe. The predominant organism at most times of the year is *Balanus amphitrite niveus* Darwin and this was accordingly selected for observation.

Results

The results of the first rotating disc experiment indicated that the approximate minimum current velocity required to prevent barnacle attachment is 1.1 knots. The disc used was 13 inches in diameter and was rotated at 540 r.p.m. The disc, together with its stationary control, are shown in Figure 1 as they appeared at the end of this experiment. Five barnacles attached to the center of the rotated disc during 23 days but did not grow beyond 2 mm. in greatest width. The limiting velocity was calculated from the $3/4$ inch diameter of the circle to which the barnacle attachments were restricted (Table I).

TABLE I

Effect of water currents upon attachment of Balanus amphitrite as observed on the lower surface of a horizontal rotating disc

Disc	Date of start	Duration of rotation (Days)	Speed of rotation (r.p.m.)	Maximum diameter at which attachment occurred (Inches)	Maximum nominal velocity at which attachment occurred (Knots)
1 B	8/20/43	23	540	3/4	1.1
4 A	11/4/43	16	192	2	1.0
6 A	12/7/43	14	134	2½	0.9
7 A	1/5/44	19	60	8	1.3
Average	—	—	—	—	1.1

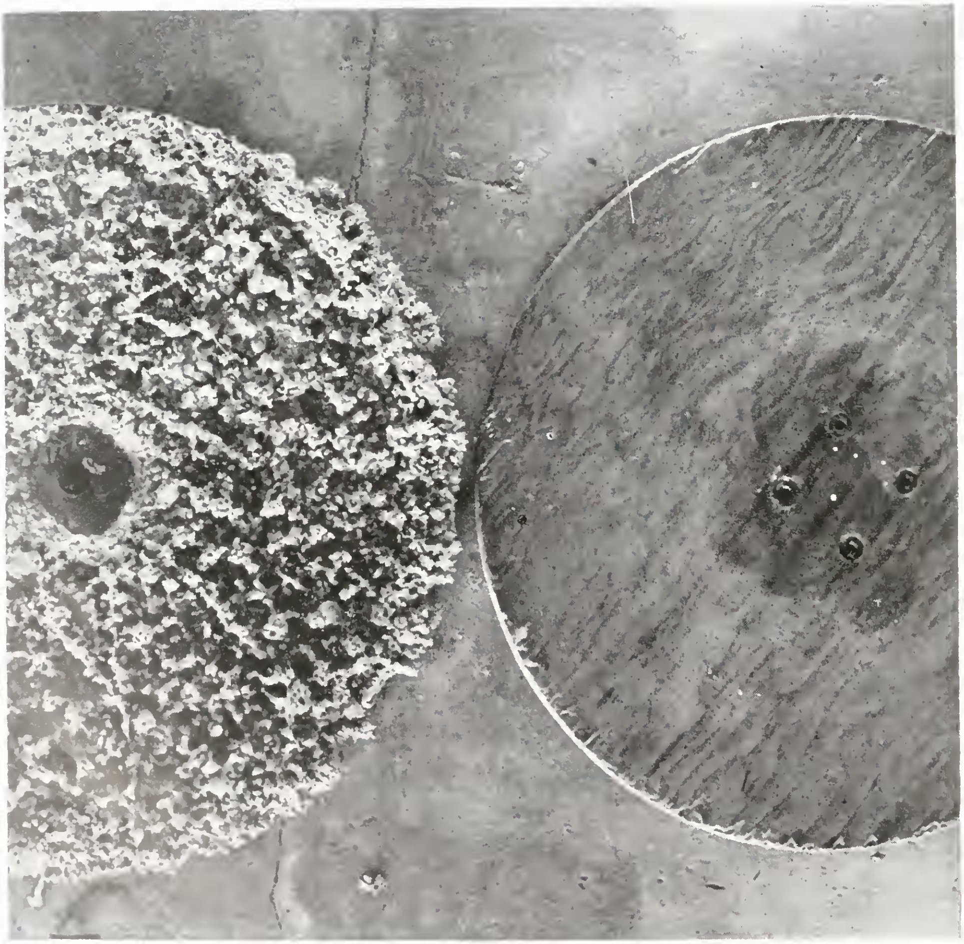

FIGURE 1. Surface of disc rotated at 540 r.p.m. for a period of 23 days, together with stationary control. Diameter of disc, 13 inches.

In order to establish the limiting velocity with greater accuracy the experiment was repeated on three other occasions at slower speeds of rotation, with the results shown in Table I and Figure 2. The nominal velocity limiting barnacle attachment as shown by these experiments varied from 0.9 knots to 1.3 knots with an average of 1.1 knots. In addition to the adverse effect upon barnacle attachment it was noticed that slime film development was greatly reduced on the rotated disc.

Attachment in Glass Tubes

Owing to the difficulty of accurately measuring the rate of water flow along the surface of the rotating disc, an independent method of investigating the relation between water currents and fouling incidence was used. In this case sea water was passed through sections of glass tubing of varying diameter (Fig. 3). Comparison of fouling incidence in each sector was made with the varying linear velocity of the water, calculated on the assumption that linear rate of flow through tubes varies inversely as the square of the diameter of cross-section. In order to estimate errors which might be introduced by virtue of turbulent flow, carmine was introduced into the water during a preliminary test run. It was observed that flow in the main portion of each section was smooth. Areas near to the joints, where turbulence was noted, were not included in the experimental observations of fouling incidence.

The tubes were approximately eight inches long and of 5 cm., 3.7 cm., 2.8 cm., 2.2. cm., and 1.4 cm. internal diameter respectively and were joined by means of fitted rubber stoppers. Attachment of barnacle larvae was encouraged by excluding direct sunlight. The water flow was provided by means of a centrifugal pump, with the experimental tubes arranged on the inlet side in order to avoid possible mechanical damage to the larvae.

While the apparatus was in operation the rate of flow was checked daily by volumetric measurement at the outlet. At the conclusion of each test run the tubes were carefully examined for signs of fouling.

Results

Observations on the glass tubes showed that limiting velocities for attachment of *Balanus amphitrite* were between 0.5 and 1.0 knot. During the first experiment with this apparatus, sea water was run through it at a rate between 13 and 16 liters per minute, on a catwalk extending over the water at the University of Miami Marine Laboratory. Fluctuations in the height of tide and consequently the suction head of the seawater pump gave rise to this fluctuation in current velocity. Barnacles attached in the two larger tubes within ten days after beginning the experiment. From the calculated linear velocity of the narrower of these tubes it appeared that barnacles are not prevented from attachment by currents varying between 0.5 and 0.6 knot (Table II). In the next smaller tube where no barnacles attached the rate of flow varied from 0.8 to 1.0 knot. The limiting velocity therefore lies between 0.5 knot and 1.0 knot. The appearance of the tubes at the end of a similar experiment is illustrated in Figures 3 and 4. The upper figure of the limits is lower than the critical velocity as measured on the rotating disc. However, in view of the difference in hydrodynamical conditions involved in the two methods, which was discussed previously, the results appear to be reasonably consistent.

FIGURE 2. Portion of disc rotated at 192 r.p.m. for a period of 16 days, showing barnacles attached at center. Diameter of disc, 24 inches.

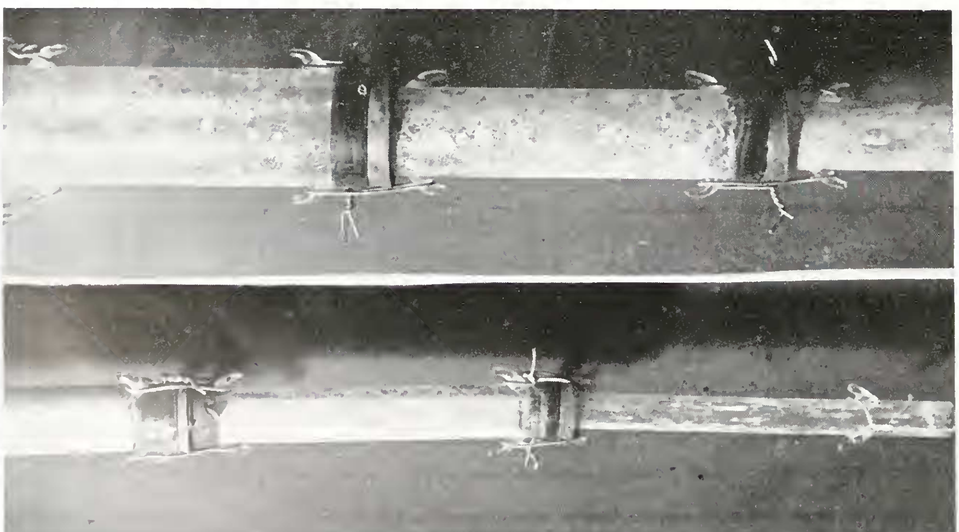

FIGURE 3. Series of five tubes of increasing cross-sectional diameter. Shows development of barnacles in wider tubes only, following prolonged passage of sea-water.

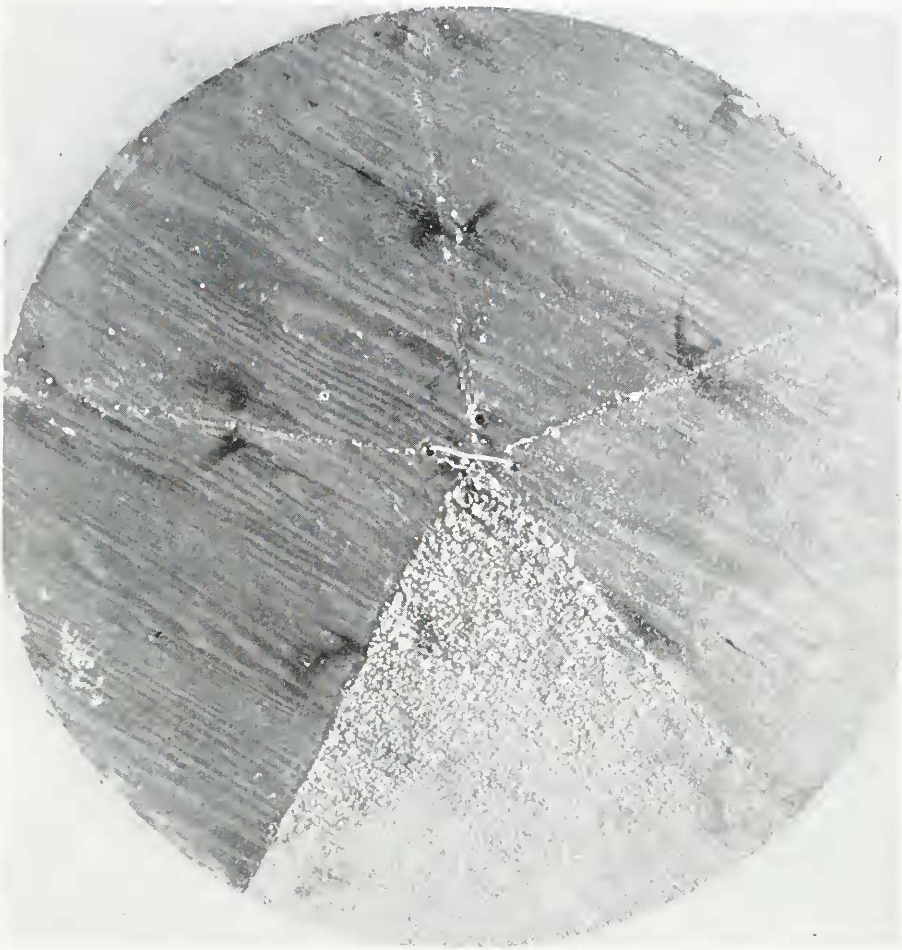

FIGURE 4. Surface of disc following 16 days of stationary immersion beginning January 8, 1944. Individual sectors of the disc were exposed for periods of 6 hrs., 1 day, 2 days, 5 days and 16 days. Diameter of disc, 28 inches.

At a later date the glass tubes were exposed at Kure Beach, N. C., by Mr. F. L. LaQue and Dr. W. Clapp, under conditions allowing a more constant flow of sea water. By reducing the flow of water in successive experiments the critical velocity for attachment was confined more closely between 1.1 and 1.3 knots for *Balanus improvisus* and below 0.8 knot for *B. eburneus*. These results are included in Table II with the permission of LaQue and Clapp.

Confirmatory results have been reported by Turner (1945) from an experiment recently conducted at Kure Beach in which a system of steel pipes of graded diameter was exposed to sea water circulation for 98 days. Fouling with mussels, barnacles, and tube worms occurred where the current velocity was one knot or less but not where it was 1.8 knots or greater.

TABLE II

Attachment of Balanus species upon vertical glass tubes of graded diameter during the passage of sea-water

Period and place	Rate of flow. Liters per minute	Equivalent velocity in glass tubes (Knots)				
		1.4 cm. diameter	2.2 cm. diameter	2.8 cm. diameter	3.7 cm. diameter	5.0 cm. diameter
11/17/43 to 11/27/43 Miami Beach	13–16	3.0–3.7 —	1.2–1.6 —	0.8–1.0 —	0.5–0.6 *B. amphitrite*	0.2–0.3 *B. amphitrite*
5/20/44 to 7/12/44 Kure Beach*	21	5.3 —	2.3 —	1.4 —	0.8 Balanus sp.	0.4 Balanus sp.
7/12/44 to 9/18/44 Kure Beach*	12.7	3.2 —	1.3 —	0.8 Balanus sp.	0.5 Balanus sp.	0.2 Balanus sp.
9/18/44 to 11/25/44 Kure Beach*	10.8	2.7 —	1.1 *B. improvisus*	0.7 *B. improvisus*	0.4 *B. eburneus* *B. improvisus*	0.2 *B. eburneus* *B. improvisus*

* Observations by W. F. Clapp and F. L. LaQue.

GROWTH ON THE ROTATING DISC

For the purpose of studying the effect of water currents upon barnacles already attached the rotating disc procedure was modified. Both rotating and stationary discs were allowed a preliminary period of stationary immersion during which barnacles became attached. Equal sectors of the disc were temporarily protected by means of cloth attached with thumb tacks. The cloth was removed from each sector after increasing intervals of time with the result that at the end of the preliminary period of immersion the maximum age of the organisms attached to the different parts of the disc varied from 16 days to 6 hours. The barnacles on each sector were then counted and the maximum diameter of the largest barnacle in each sector was measured.

Following the period of stationary immersion the control disc was allowed to remain in a stationary position and the other was placed on the rotating shaft for a further period. Both discs were examined and the number of barnacles per square inch and their greatest diameter were recorded separately for each sector and for areas at successive distances from the center of the disc.

Results

The first experiment of this series provided an initial 16 days' period of stationary immersion during which both experimental and control discs became seeded with barnacles. At the end of this period barnacles had been attached on the five sectors for maximum periods of 6 hours, 1 day, 2 days, 5 days, and 16 days respectively (Fig. 4). Immediately following the period of stationary growth, the experimental disc was rotated at an angular velocity of 60 r.p.m. for 19 consecutive days, while the control disc was allowed to remain in a stationary position for the same period. The appearance of both discs at the end of the experiment is shown in Figures 5 and 6.

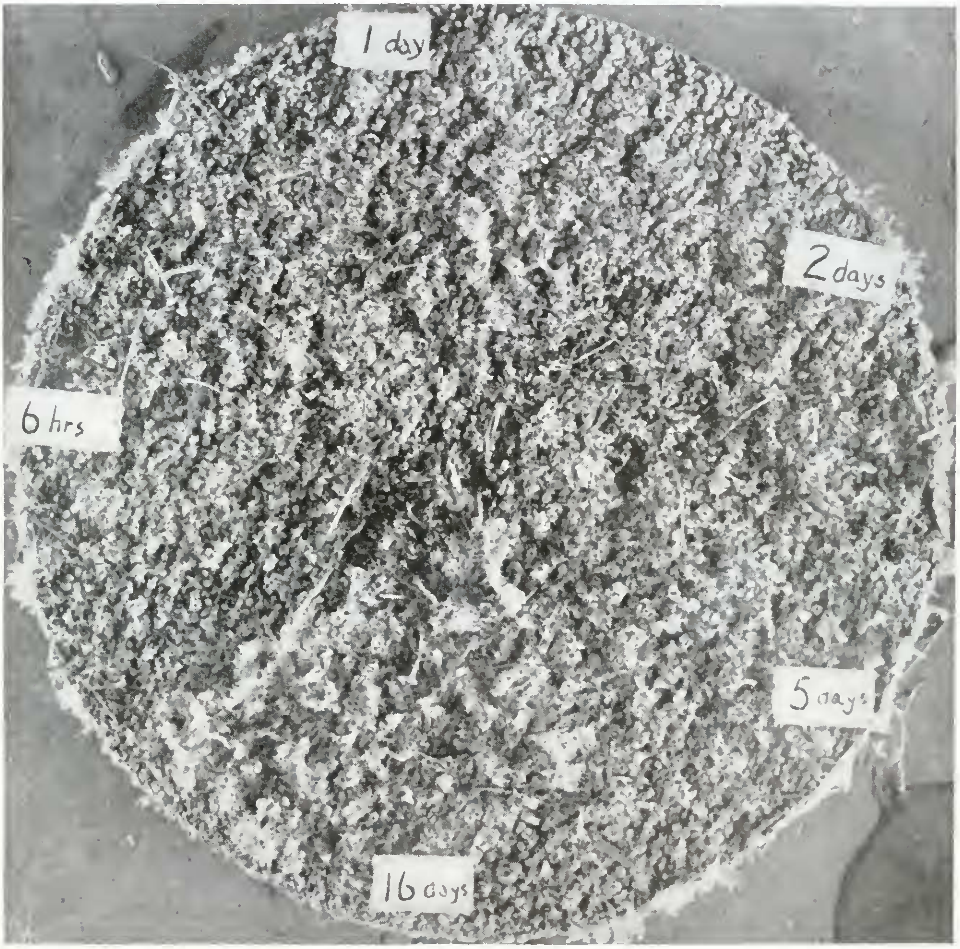

FIGURE 5. Same disc as in Figure 4 after further period of 19 days stationary immersion. Control to disc shown in Figure 6.

Examination of the discs at the conclusion of the test showed that while increasing current velocities diminished the growth rate and finally brought about loss of attachment, the weaker currents appeared to enhance growth. Thus, when rotated on Sector I, where growth had continued for 6 hours before rotation, *B. amphitrite*

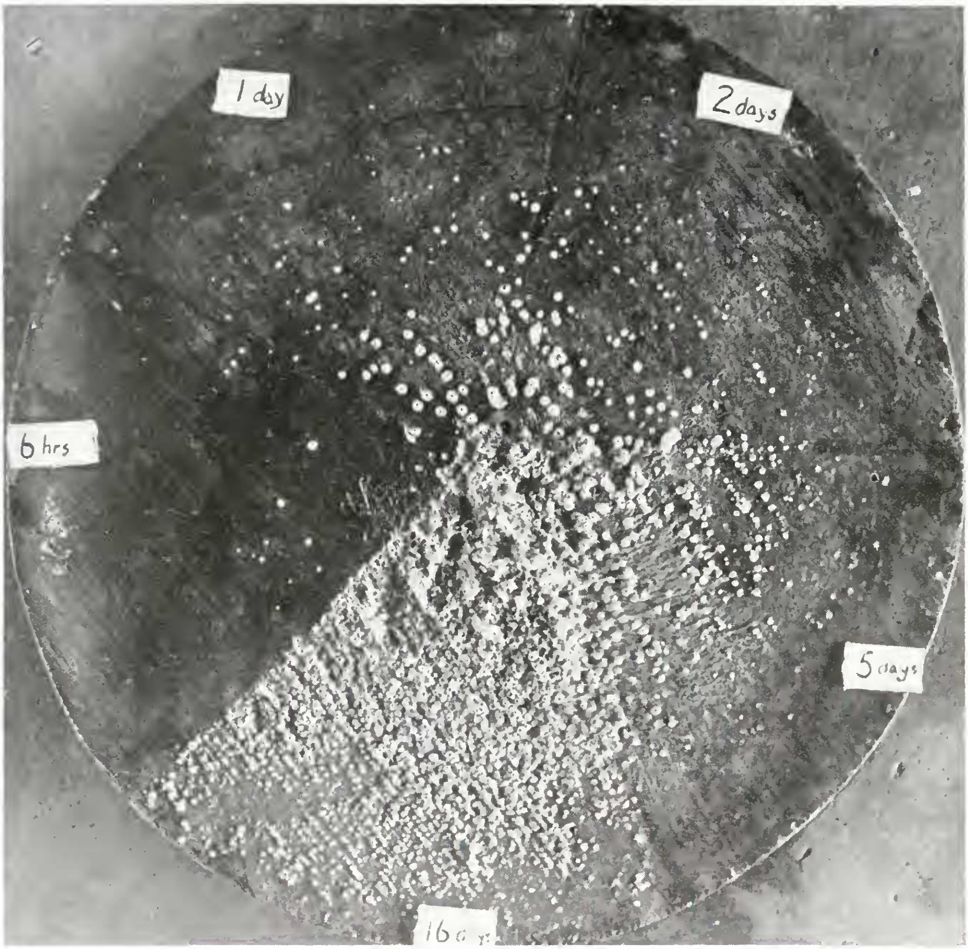

FIGURE 6. Similar disc to that of Figure 4 after period of 19 days rotation at 60 r.p.m. Age of barnacles before rotation is marked on each sector.

neither continued development nor remained attached at diameters beyond 16 inches, corresponding to a current of 2.7 knots (Table III). Within Sector VI, however, with barnacles originally 16 days old, a small number remained attached even at the outer edge of the disc, where the water flow approximated 4.7 knots. On the intervening sectors with barnacles of intermediate ages, the current velocities bringing about complete loss of attachment showed values between these extremes. Probably because of further attachments on the stationary control, the density of attachments on all sectors of the rotated disc was below that of the control.

The effects upon growth rate are illustrated by the observations in Table IV. On Sector I, within a 4 inch diameter, equivalent to 0.7 knot, barnacles reached a maximum width of 8 mm., compared with growth on the control of only 7 mm. At 2.3 knots, growth was reduced to only 3 mm. and at 2.7 knots, no barnacles re-

TABLE III

Effect of water currents upon adhesion of barnacles of different ages when subjected to 19 days rotation upon a submerged disc, as shown by density of attachment in number per square inch. Experiment initiated January 8, 1944

Position on disc		Age before rotation				
Diameter (Inches)	Nominal water velocity (Knots)	Sector I (6 hours)	Sector II (1 day)	Sector III (2 days)	Sector IV (5 days)	Sector V (16 days)
0–28*	0	Dense	Dense	Dense	Dense	Dense
4	0.7	1.7	1.7	1.7	2.0	Too crowded to count
6	1.0	0	0.4	0.9	1.7	
8	1.3	0	0.4	1.0	1.3	
10	1.7	0.1	0.4	1.0	1.0	
12	2.0	0.2	0.4	0.6	1.9	
14	2.3	0.1	0.4	0.9	1.3	
16	2.7	0	0.4	0.6	0.9	
18	3.0	0	0.1	0.2	0.6	
20	3.3	0	0	0.1	0.4	
22	4.0	0	0	0	0	
28	4.7	Few in cracks	0	Few in cracks	Few in cracks	Few

* Stationary control.

mained on the sector. At intermediate current velocities conditions of growth lay between these two extremes, with normal growth occurring between 0.7 and 1.7 knots.

Similar observations were made upon barnacles of greater initial age within the remaining sectors. Thus, on Sector IV, where development had continued for a maximum period of 5 days before rotation, barnacles showed enhanced growth rate in currents up to one knot, normal growth similar to that of the control up to 2 knots, and almost complete cessation of growth at 3.3 knots. No barnacles remained on this sector at 4 knots.

Similar conditions of enhanced growth at low velocities, normal growth at intermediate velocities and cessation of growth with loss of attachment at higher velocities were observed on the remaining sectors, with barnacles of different initial ages.

The anomalous absence of enhanced growth on Sector V is probably due to the crowded condition of the barnacles which had become attached during a 16 day stationary period. The one day old barnacles were apparently less affected by the

TABLE IV

Effect of water currents upon growth of barnacles of different ages when subjected to 19 days rotation upon a submerged disc, as shown by diameter of largest barnacle in millimeters. Experiment initiated January 8, 1944

Position on disc		Age and size before rotation				
Diameter (Inches)	Nominal water velocity (Knots)	Sector I 6 hours (<1 mm.)	Sector II 1 day (<1 mm.)	Sector III 2 days (<1 mm.)	Sector IV 5 days (2 mm.)	Sector V 16 days (5 mm.)
0–28*	0	7 mm.	7 mm.	8 mm.	8 mm.	9 mm.
4	0.7	8 mm.	8 mm.	8 mm.	9 mm.	
6	1.0	—	8 mm.	9 mm.	9 mm.	
8	1.3	—	8 mm.	8 mm.	8 mm.	
10	1.7	6 mm.	7 mm.	6 mm.	8 mm.	None more than 8 mm.
12	2.0	5 mm.	5 mm.	6 mm.	8 mm.	
14	2.3	3 mm.	6 mm.	4 mm.	6 mm.	
16	2.7	—	5 mm.	3 mm.	5 mm.	
18	3.0	—	1.5 mm.	1.5 mm.	4 mm.	7 mm.
20	3.3	—	—	1.5 mm.	2.5 mm.	6 mm.
24	4.0	—	—	—	—	6 mm.
28	4.7	1.5 mm.	—	1.5 mm.	4 mm.	5 mm.

* Stationary control.

inhibitory action of water currents than the two day old barnacles. Otherwise, the adverse effects of water currents increased with their velocity, and decreased with the initial age of the barnacles.

On all sectors a few barnacles continued to grow at the perimeter of the disc where the presence of cracks provided local flow pockets with relatively still water.

The first experiment demonstrated an actual loss of barnacles at current velocities having critical values for the different initial ages of barnacles. In order to determine the time required for the loss of attachment to occur, a second experiment was carried out in which the disc was examined, not only at the beginning and end of the rotation period, but also at intervening times. The density of attachment and maximum size of barnacles were observed at each examination, as in the previous experiment.

The experiment was carried out during a period of heavy barnacle set. At the end of the stationary period, extending from February 19 to March 1, 1945, the density of attachments upon each sector, and particularly upon the sectors longest exposed, was very much greater than in the previous experiment.

TABLE V

Density of barnacle attachment compared with rate of flow of water relative to the surface of a rotating disc, expressed in number per square inch *
(Figures in brackets indicate density upon a stationary panel serving as control; D, *over 75 per square inch)*

Stationary growth period	Diameter of disc (Inches)	Velocity (Knots)	Period of rotation							
			0 hrs.	1 hr.	12 hrs.	3 days	5 days	7 days	9 days	11 days
Sector I	Control	(0)	(30)	(30)	(30)	(30)	(30)	(60)	(D)	(D)
	4	1.5	30	25	25	20	15	10	8	5
	8	3	30	30	20	20	15	10	8	6
6 hrs.	12	5	30	30	20	20	15	6	6	6
	16	6.5	30	30	20	20	15	6	6	5
	20	8	30	30	20	20	15	4	4	2
	24	10	35	30	20	20	12	4	4	2
Sector II	Control	(0)	(30)	(30)	(30)	(30)	(30)	(60)	(D)	(D)
	4	1.5	30	30	30	30	20	15	15	8
	8	3	30	30	30	30	20	15	15	12
12 hrs.	12	5	30	30	30	30	20	15	15	6
	16	1.5	30	30	30	30	20	15	15	6
	20	8	30	30	30	30	20	10	10	5
	24	10	30	30	30	10	7	7	7	4
Sector III	Control	(0)	(30)	(30)	(30)	(30)	(30)	(60)	(D)	(D)
	4	1.5	30	30	30	20	20	12	12	10
	8	3	30	30	30	20	20	12	12	12
1 day	12	5	30	30	30	20	12	10	10	10
	16	6.5	30	30	30	20	12	10	10	6
	20	8	30	30	30	20	12	7	7	5
	24	10	30	30	30	7	5	5	4	4
Sector IV	Control	(0)	(30)	(30)	(30)	(40)	(40)	(50)	(D)	(D)
	4	1.5	30	30	30	20	20	17	17	15
	8	3	30	30	30	24	20	20	20	19
2 days	12	5	30	30	30	24	20	20	15	9
	16	6.5	30	30	30	24	20	20	15	8
	20	8	30	30	30	15	10	10	10	7
	24	10	30	30	30	10	7	7	6	6
Sector V	Control	(0)	(30)	(30)	(30)	(50)	(50)	(D)	(D)	(D)
	4	1.5	35	35	35	32	32	32	30	30
	8	3	35	35	30	30	30	30	30	30
	12	5	35	35	30	30	30	30	30	24
5 days	16	6.5	35	35	30	30	30	30	30	15
	20	8	35	35	30	30	30	30	30	15
	24	10	35	35	25	25	25	25	25	15
Sector VI	Control	(0)	(70)	(70)	(70)	(70)	(D)	(D)	(D)	(D)
	4	1.5	75	75	75	75	75	75	75	50
	8	3	75	75	75	70	70	70	70	30
10 days	12	5	75	75	75	70	70	70	70	30
	16	6.5	75	75	75	70	70	70	70	25
	20	8	75	75	75	70	70	70	70	20
	24	10	75	75	75	70	70	70	70	20

* Experiment initiated 2/19/45.

Observations showed that, as in the previous experiment, losses in attached barnacles occurred roughly in proportion to the current velocity, although at no point of the disc was the entire set lost. Similarly, the limiting rate of flow necessary for inhibition of growth or for loss of attachment increased generally with the initial age of the barnacles. Since observations were made at intervals during the experiment it was also possible to note the period of rotation necessary to bring about the first losses in attachment. This also increased generally with increasing age of initial growth. The observations are set forth in detail in Tables V and VI and summarized in Table VII.

In Table V the number of barnacles per square inch is recorded for various distances from the center of the disc, and for each individual sector. These observations are repeated for various intervals of time during the experiment.

An increase took place in numbers on the control panels due to continued attachment of cyprids, whereas on the rotated disc barnacles became progressively reduced in number as the experiment continued. After one hour of rotation the only losses were among the six hour old barnacles on Sector I. These losses were very small, however, and although observed at current velocities of 1.5 knots and 10 knots, they did not occur at intervening velocities. The first significant losses took place twelve hours after the start of rotation among barnacles less than twelve hours old. Of the older ones, only those 5 days old showed losses, amounting to a change at most velocities from 35 to 30 per unit area.

Barnacles on the remaining sectors, varying in age from twelve hours upwards, were not observed to diminish in number until the third day of rotation. The smallest loss over this period took place among the twelve hour barnacles, which were only lost at speeds of ten knots, whereas, after a similar period of rotation, other barnacles of greater ages had been lost even at 1.5 knot current velocity. Ten day old barnacles were not greatly disturbed by 1.5 knot currents until after eleven days' rotation. These observations, summarized in Table VII, indicate that in general the velocity of current necessary to dislodge barnacles increased with the age they had reached before the experiment. Barnacles twelve hours old, however, showed a marked increase in resistance to being dislodged, even compared to those ten days old, whereas those two days old, on the other hand, seemed to be less resistant than younger or older ones. It is also noteworthy that in general the duration of rotation necessary to bring about the first losses depends much more upon the initial age of the barnacle than upon the current velocities.

In a similar manner the percentage of the original number of barnacles remaining following an eleven day period of rotation increased with increasing age before rotation. The ten day old barnacles at the end of the experiment, however, showed poorer resistance and had a lower percentage of continued attachment than in the case of the five day barnacles. It must be noted, however, that the ten day barnacles were densely crowded and it is possible that this factor decreased their resistance to dislodgement.

Further examination of the results in Table V discloses that losses continued to occur to some extent on all sectors at the end of eleven days, although they were less on those sectors where initial age of the barnacle was greater.

Observations of the size of barnacles recorded during the experiment are given in Table VI. On Sector I the six hour old barnacles within a diameter of 8 inches, equivalent to a three knot water current, continued to grow, although at a slow rate.

TABLE VI

*Growth of barnacles in relation to flow of water over the surface of a rotating disc, expressed as greatest diameter in millimeters **
(Figures in brackets refer to stationary control)

Stationary growth period	Diameter of disc (Inches)	Velocity (Knots)	Period of rotation							
			0 hrs.	1 hr.	12 hrs.	3 days	5 days	7 days	9 days	11 days
Sector I	Control	(0)	(0.3)	(0.3)	(0.3)	(0.5)	(0.8)	(1.3)	(2.5)	(3.0)
	4	1.5	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.5
	8	3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
6 hrs.	12	5	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	16	6.5	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	20	8	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	24	10	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
Sector II	Control	(0)	(0.3)	(0.3)	(0.3)	(0.6)	(0.8)	(2.5)	(3.0)	(3.5)
	4	1.5	0.3	0.3	0.3	0.3	0.3	0.3	1.0	1.5
	8	3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
12 hrs.	12	5	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	16	6.5	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	20	8	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	24	10	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
Sector III	Control	(0)	(0.3)	(0.3)	(0.3)	(0.6)	(0.8)	(2.0)	(3.0)	(3.5)
	4	1.5	0.3	0.3	0.3	0.5	0.5	1.0	2.0	3.0
	8	3	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5
1 day	12	5	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5
	16	6.5	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5
	20	8	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5
	24	10	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5
Sector IV	Control	(0)	(0.3)	(0.3)	(0.5)	(0.8)	(1.0)	(3.0)	(3.5)	(4.0)
	4	1.5	0.3	0.3	0.5	1.0	1.0	1.3	1.3	1.5
	8	3	0.3	0.3	0.3	0.8	0.8	0.8	0.8	1.0
2 days	12	5	0.3	0.3	0.3	0.8	0.8	0.8	0.8	1.0
	16	6.5	0.3	0.3	0.3	0.3	0.8	0.8	0.8	0.8
	20	8	0.3	0.3	0.3	0.3	0.8	0.8	0.8	0.8
	24	10	0.3	0.3	0.3	0.3	0.8	0.8	0.8	0.8
Sector V	Control	(0)	(0.8)	(1.0)	(1.5)	(2.5)	(3.0)	(4.0)	(5.0)	(6.0)
	4	1.5	0.5	0.8	1.0	2.5	2.5	3.0	3.0	3.5
	8	3	0.5	0.8	0.8	1.5	1.5	1.5	1.5	1.5
5 days	12	5	0.5	0.5	0.8	1.5	1.5	1.0	1.5	1.5
	16	6.5	0.5	0.5	0.8	1.5	1.5	1.0	1.5	1.5
	20	8	0.5	0.5	0.8	1.5	1.5	1.0	1.5	1.5
	24	10	0.5	0.5	0.8	0.8	0.8	0.8	0.8	0.8
Sector VI	Control	(0)	(2.5)	(2.0)	(2.5)	(4.0)	(5.0)	(7.0)	(9.0)	(9.0)
	4	1.5	2.0	2.0	2.0	3.5	3.5	4.5	4.5	5.0
	8	3	2.0	2.0	2.5	3.0	3.0	3.5	3.5	3.5
10 days	12	5	2.0	2.0	2.0	3.0	3.0	3.5	3.5	3.5
	16	6.5	2.0	2.0	2.0	3.0	3.0	3.5	3.5	3.5
	20	8	2.0	2.0	2.0	3.0	3.0	3.5	3.5	3.5
	24	10	2.0	2.0	2.0	3.0	3.0	3.5	3.5	3.5

* Experiment initiated 2/19/45.

TABLE VII

*Summary of observations on the effect of water currents produced by rotation upon attached barnacles. Expressed as multiples of normal growth, period before loss in number first occurred, and percentage remaining at the end of eleven days **

Current velocity (Knots)	Period of stationary growth					
	6 Hrs.	12 Hrs.	1 Day	2 Days	5 Days	10 Days
1.5	0.1 × (1 Hour) 20%	0.4 × 5 Days 30%	0.8 × 3 Days 30%	0.3 × 3 Days 50%	0.6 × 3 Days 90%	0.6 × 11 Days 70%
3	*Inhibition* 12 Hours 30%	*Inhibition* 5 Days 40%	*Inhibition* 3 Days 40%	0.3 × 3 Days 60%	0.2 × 2 Days 90%	0.3 × 3 Days 40%
5	— 12 Hours 20%	— 5 Days 20%	— 3 Days 30%	0.1 × 3 Days 30%	0.2 × 2 Days 70%	0.3 × 3 Days 40%
6.5	— 12 Hours 20%	— 5 Days 20%	— 3 Days 20%	*Inhibition* 3 Days 30%	0.2 × 2 Days 60%	0.3 × 3 Days 30%
8	— 12 Hours 20%	— 5 Days 20%	— 3 Days 20%	— 3 Days 20%	*Inhibition* 2 Days 60%	0.3 × 3 Days 30%
10	— (1 Hour) 10%	— 3 Days 20%	— 3 Days 20%	— 3 Days 20%	— 2 Days 60%	0.3 × 3 Days 30%

* Experiment initiated 2/19/45.

Even at velocities below 1.5 knots the growth was considerably less than that of the stationary control. The ten day old barnacles on Sector VI continued to grow near the circumference, although subjected to ten knot currents. Barnacles of intermediate age showed a reduction of growth inversely dependent upon their initial age, and directly dependent upon the current. Barnacles less than two days old ceased growth at water currents over three knots, and only the ten day old barnacles continued growth at ten knots.

At the end of this experiment the remaining barnacles were examined to determine whether any considerable portion remaining attached was dead. A few of the older barnacles had lost their soft parts, but it was difficult to obtain a reliable criterion as to the condition of the remainder. It was not definitely established, therefore, what proportion had died.

Differences between the results of this and the previous experiment lie mainly in the higher current velocities required to bring about growth inhibition and loss of attachment and the absence of complete loss at any part of the disc in the later experiment. This apparent anomaly may be partly due to the much greater density of initial attachment, which may have reduced the *effective* velocity of the currents by providing a much more irregular surface. It is also conceivable that had the experiment continued for the full 19 day period of the first experiment rather than 11 days only, the growth inhibition effect might have appeared at lower velocities and might have resulted in complete loss at some parts of the disc.

Discussion

The experimental results indicated that current velocities limiting the attachment of barnacles lie in the neighborhood of one knot and that the limits for the three species, *Balanus eburneus, B. amphitrite,* and *B. improvisus* are in ascending order of magnitude. That a one knot current should limit attachment is in accordance with the conclusions of Visscher and earlier workers that attachment of barnacles does not readily take place upon ships in motion.

It further appears that growth rates of previously attached barnacles are reduced by water currents in inverse proportion to the age of the barnacle and directly in proportion to the current velocity. The effect of crowding together is further to reduce the growth rate. The effect of very low current velocities is to increase the rate of growth. A slight loss of attachment occurs at all current velocities, but this may be partly due to overcrowding. Large and significant losses take place at velocities which are sufficient to reduce the growth rate. These losses begin some hours after the start of rotation, and continue for a period of at least eleven days.

Since losses due to dislodgement do not occur during the first few hours of rotation, except in the case of barnacles attached within six hours or less, and since they continue to take place during the entire period of rotation, it seems probable that they are not directly due to mechanical action. Possibly the mechanism is one of interference with feeding processes, followed by reduced growth rate, death and diminished adhesion.

A further point arising out of the experimental data is the fact that at equivalent current velocities 12 hour and 24 hour old barnacles show greater growth and less loss of attachment than those somewhat older. It is possible that at this stage of development, with metamorphosis incomplete, an orientation to the current may occur which facilitates feeding, although this was not actually observed.

Once attached the barnacles are able to withstand current velocities of increasing magnitude, although for the first two or three weeks the growth rate is considerably reduced. Loss of attachment appears to follow reduced growth rate and may involve actual death from lack of food. The current velocities required to bring this about are sufficiently low to provide support for Visscher's conclusion that barnacles are killed by ocean passages of 500 miles or more, if vessels of more than 10 knots performance are considered, or if the age of attached barnacles is no greater than a 10 day stay in port would allow. On the other hand, current velocities lying below this figure, such as would be produced by slow sailing vessels, would appear from the experimental data to be insufficient to bring about a loss of the attached barnacles. In the case of faster ships, stays in port of longer than a few days might also permit the accumulated barnacles to survive an ocean passage. This type of ship service would readily provide a means of distribution for barnacles. It would explain Fischer-Piette's observations of the appearance of *Balanus amphitrite* on Mediterranian shores, and would support his hypothesis of distribution by ships.

The enhanced growth rate in current velocities of 1.3 knots and less, depending on the age of the barnacle, provides a quantitative expression for the observations of Rice, Moore, Kitching, and others upon the increased growth of barnacles subjected to water currents.

The conditions in a harbor or an embayed or open coast are rarely such that tidal currents in excess of one knot are continuously present. Under these conditions, therefore, there would be no obstacle to the attachment of barnacles. Once attached, however, the barnacles would usually be subjected to intermittent tidal currents.

No data are available as to the effects of intermittent currents but it would be reasonable to assume that these would be, if anything, less than the effects of continuous currents. The data presented here would therefore make it appear unlikely that any but the strongest of tidal currents would prevent the attachment and continued development of barnacles on rocks or stone, and wooden piling. Where fairly continuous currents of less than 1.5 knots were present the growth would be encouraged.

A different situation occurs in estuaries where continuous currents might occur. Here, however, the limiting factor, according to the work of previous authors, is probably lowered salinity, since continuous currents would scarcely permit of the estuary remaining salt.

Where wave action is strong the effects might be considered as equivalent to strong currents of frequently changing direction, which might conceivably inhibit attachment or growth, even below tide levels. Even where attachment occurred during temporary lulls, the strong recurrent wave action might be expected to dislodge the barnacles. This may explain the observations of Stephenson and his co-workers that some species of barnacles do not occur in a zone of heavy wave action.

The effect of water currents under natural conditions may therefore be summarized as one of enhanced growth with velocities below 1.5 knots, and one of reduced growth above this. It would rarely happen under natural conditions that water currents alone would prevent barnacle colonization. Strong wave action, however, might be expected to have this effect.

Certain qualifications should be added to the above discussion which may explain some anomalous observations. The arguments above are based on the calculated rates of flow of water over the rotating disc, and the results of experiments have indicated that these rates are slightly higher than the actual rates of flow taking place. The error, however, does not appear to be greater than 10 per cent to 20 per cent, and does not qualitatively affect the validity of the general conclusions.

Since the observations were made upon the relatively smooth surface of a wooden disc, they would not be applicable to very rough surfaces where local pockets of relatively still water might develop, to the areas immediately adjacent to lapped plates of ships' hulls, or to portions of piling or other submerged surfaces where the contours and configuration might produce local stagnation effects.

Summary

1. The work of previous authors, dealing with the effect of water currents upon barnacle attachment, growth and distribution is briefly reviewed.

2. Experiments were conducted to determine the effects of water currents upon the attachment and growth of barnacles, and particularly of *Balanus amphitrite*.

Submerged rotating discs and glass tubes of graded cross-sectional diameter were employed to provide variations in current velocity.

3. The velocity of water current limiting attachment appears to lie between 0.5 and 0.9 knot for *Balanus amphitrite,* between 0.4 and 0.7 knot for *B. eburneus,* and above 1.1 knots for *B. improvisus.*

4. Following attachment the growth rate of barnacles was found to be increased by water currents of velocity less than 1.5 knots and to be decreased by currents with velocities in excess of this. The adverse effects of water currents were found to decrease with increasing age of the barnacles subsequent to attachment. Six hours after attachment, growth rate was reduced to one-third of normal by a 1.5 knot current and completely stopped by a 3 knot current. Five days after attachment, growth was prevented by currents ranging between 3.3 and 8 knots.

Loss of attachment appeared to some extent among all barnacles in which growth rate was reduced. This loss was greatest at velocities bringing about complete cessation of growth.

5. It is suggested that loss of attachment is due to interference with the feeding process, followed by reduction of growth rate, death, and diminished adherence. Possibly due to an orientation to the current which facilitates feeding, barnacles attached for one day or less show less retardation of growth rate and loss of adherence than barnacles two days old.

6. Since tidal currents are almost invariably intermittent it appears from the data presented that they are not sufficient to prevent the colonization of suitable surfaces by barnacles, except where the velocities are unusually high.

It also follows from the numerical results obtained that on vessels making short stays in port and relatively long voyages, little permanent barnacle fouling will occur, since those organisms which attach will be killed and at least a portion of them dislodged. The evidence does not preclude, however, the continued growth of barnacles upon slow vessels making longer stays in port, and their geographical distribution by this means.

LITERATURE CITED

Bright, K. M. F., 1938. The South African intertidal zone and its relation to ocean currents. II, III. Areas of the west coast. *Trans. Roy. Soc. S. Africa,* **26**: 49–88.

Bokenham, N. A. H., and T. A. Stephenson, 1938. The colonization of denuded rock surfaces in the intertidal region of the Cape Peninsula. *Ann. Natal Mus.,* **9**: 47–82.

Eyre, J., 1939. The South African intertidal zone and its relation to ocean currents. VII. An area in False Bay. *Ann. Natal Mus.,* **9**: 283–306.

Eyre, J., and T. A. Stephenson, 1938. The South African intertidal zone and its relation to ocean currents. V. A sub-tropical Indian shore. *Ann. Natal Mus.,* **9**: 21–46.

Eyre, J., Brock Ruysen, G. J., and M. I. Crichton, 1938. The South African intertidal zone and its relation to ocean currents. VI. The East London district. *Ann. Natal Mus.,* **9**: 83–112.

Fischer-Piette, E., 1928. Recherches de bionomie et d'oceanographie littorales sur la Rance et le littoral de la Manche. *Ann. Inst. Oceanogr. Monaco,* n. s. **5**: 201–429.

Fischer-Piette, E., 1928 (a) Sur la distribution geographique de quelques organismes de rocher, le long des côtes de la Manche. *Maritime Mus. Nat. Hist. Natur. Saint-Servan,* II. Trav. du Lab.

Fischer-Piette, E., 1929. Le cirripede Balanus amphitrite Darwin à Saint-Servan. *Bull. Lab. Maritime Saint-Servan,* **4**: 10–11.

Fischer-Piette, E., 1932. Repartition des principales espèces fixées sur les rochers battus des côtes et des iles de la Manche, de Lannion à Fécamp. *Ann. Inst. oceanogr. Monaco,* n. s. **12**: 105–213.

Fischer-Piette, E., 1935. Quelques remarques bionomiques sur la côte basque française et espagnole. *Bull. Lab. Maritime Saint-Servan,* **14**: 1–14.

Hentschel, E., 1924. Das Werden und Vegehen des Bewuches an Schiffen. *Mitt. Zool. Mus. Hamburg,* **41**: 1–51.

Hiraga, Yuzuru, 1934. Experimental investigations on the resistance of long planks and ships. *Zosen Kiokai (J. Soc. Naval Arch. Japan),* **55**: 159–199.

LaQue, F. L., 1943. Proving ground of Marine Corrosion. *Inco Magazine,* **19**: 4–7.

McDougall, K. D., 1943. Sessile marine invertebrates at Beaufort, North Carolina. *Ecological Monographs,* **13**: 321–374.

Moore, H. B., 1933. Change of orientation of a barnacle after metamorphosis. *Nature,* **132**: 969–970.

Moore, H. B., 1934. The biology of Balanus balanoides. I. Growth rate and its relation to size, season, and tidal level. *Jour. Marine Biol. Ass. U. K.,* n. s. **19**: 851–868.

Moore, H. B., 1935. The biology of Balanus balanoides. IV. Relation to environmental factors. *Jour. Marine Biol. Ass. U. K.,* n. s. **20**: 277–307.

Moore, H. B., 1936. The biology of Balanus balanoides. V. Distribution in the Plymouth area. *Jour. Marine Biol. Ass. U. K.,* n. s. **20**: 701–716.

Moore, H. B., 1939. The colonization of a new rocky shore at Plymouth. *Jour. Anim. Ecol.,* **8**: 29–38.

Moore, H. B., and J. A. Kitching, 1939. The biology of Chthamalus stellatus (Poli). *J. Marine Biol. Ass. U. K.,* n. s. **23**: 521–541.

Neu, Wolfgang, 1932. Untersuchungen über den Schiffobewuchs. *Int. Rev. Hydrobiol. Hydrogr.,* **27**: 105–119.

Neu, Wolfgang, 1933. Biologisches Arbeiten über den Schiffsbewuchs. *Int. Rev. Hydrobiol. Hydrogr.,* **29**: 455–458.

Newcombe, C. L., 1935. A study of the community relationships of the sea mussel, Mytilus edulis, L. *Ecology,* **16**: 234–243.

Phelps, A., 1942. Observations on reactions of barnacle larvae and growth of metamorphosed forms at Beaufort, N. C., June, 1941 to Sept. 1941. *Fourth semi-annual Report from Woods Hole Oceanographic Institution to Bureau of Ships.* I., Paper VII. (Unpublished.)

Pierron, R. P., and Y. C. Huang, 1926. Animal succession of denuded rocks. *Publ. Puget Snd. Biol. Sta.,* **5**: 149–157.

Prennant, M., and G. Teissier, 1924. Notes ethologiques sur la faune marine sessile des environs de Roscoff. Cirripedes, bryozoaires, hydraires. *Trav. Sta. Biol. Roscoff,* **2**: 1–24.

Rice, L., 1930. Peculiarities in the distribution of barnacles in communities and their probable causes. *Publ. Puget Snd. Biol. Sta.,* **7**: 249–257.

Shelford, V. E., and E. D. Towler. 1925. Animal Communities of the San Juan Channel and adjacent areas. *Publ. Puget Snd. Biol. Sta.,* **5**: 33–73.

Stephenson, T. A., Stephenson, A., and K. M. F. Bright, 1938. The South African intertidal zone and its relation to ocean currents. IV. The Port Elizabeth district. *Ann. Natal Mus.,* **9**: 1–20.

Stephenson, T. A., Stephenson, A., and C. A. du Toit, 1937. The South African intertidal zone and its relation to ocean currents. I. A temperate Indian Ocean shore. *Trans. Roy. Soc. S. Africa,* **24**: 341–382.

Towler, E. D., 1930. An analysis of the intertidal barnacle communities of the San Juan Archipelago. *Publ. Puget Snd. Biol. Sta.,* **7**: 225–232.

Turner, H. J. Jr. The concentrations of chlorine and sodium pentachlorphenate required for the prevention of fouling in sea water pipe systems. Interim Report No. XI from the Woods Hole Oceonographic Institution to the Bureau of Ships, Navy Department. Nov. 8, 1945. (Unpublished.)

Visscher, J. P., 1928. Nature and extent of fouling of ships' bottoms. *Bull. Bur. Fisheries,* **43** (2): 193–252.

Visscher, J. P., 1930. Fouling of ships' bottoms. 2. Factors causing fouling. 3. Methods preventing fouling. *Paint and Varn. Prod. Mgr.,* **35**, **36**.

Visscher, J. P., 1938. Some recent studies on barnacles. *Biol. Bull.,* **75**: 341–342.